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Research Article

Cuckoo wasps (Hymenoptera: Chrysididae) as overlooked hosts of pollinator pathogens: environmental context of interspecific transmission

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Pollinator decline is strongly influenced by the spread of pathogens across species, yet most research has focused on honey bees and a narrow range of managed or wild pollinators. Cuckoo wasps (Hymenoptera: Chrysididae), a diverse family of cleptoparasitic and parasitoid insects, remain unstudied in this context despite their dual role as floral visitors and nest parasites of solitary bees and wasps. This study investigated whether cuckoo wasps could host bee-associated pathogens, including viruses, microsporidia and trypanosomatids. Specimens were collected at two Italian sites with contrasting environmental conditions and analysed individually using quantitative PCR. In total, 343 hymenopterans were screened, including 84 cuckoo wasps representing 21 species. All pathogens except *Crithidia mellificae* were detected. Pathogen prevalence and abundance varied significantly between sites, with higher values of deformed wing virus (DWV) and *C. bombi* at the montane site, and greater prevalence of *Nosema ceranae* and acute bee paralysis virus (ABPV) at the lowland site, indicating strong environmental influences. Cuckoo wasps generally showed lower DWV prevalence than wild bees but higher prevalence of *C. bombi* and black queen cell virus (BQCV). Strikingly, host–parasite pairs such as *Chrysis rufitarsis* and *Hoplitis laevifrons* shared nearly the full pathogen set, suggesting direct transmission through parasitic interactions in addition to environmental and floral pathways. The obtained findings provide the first evidence that cuckoo wasps host a broad range of pollinator pathogens. By linking floral and nest-based transmission routes, cuckoo wasps may play a pivotal ecological role within pathogen networks. These results highlighted the need to include parasitic taxa in pathogen surveillance to better understand pollinator health and ecosystem resilience.

Keywords: deformed wing virus, host, parasite interactions, *Nosema ceranae*, pathogen transmission, pollinator health, spillover, trypanosomatids

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Introduction

Pollinators are crucial for the conservation of biodiversity and ecosystems (Senapathi et al. 2015, Katumo et al. 2022), human health (Potts et al. 2016), the reproduction of entomophilous angiosperms (Albrecht et al. 2012, Ratto et al. 2018), and have significant economic value due to their key role in agriculture (van der Sluijs and Vaage 2016, Khalifa et al. 2021, Lippert et al. 2021, Saha et al. 2023). However, their decline is well-documented and primarily driven by anthropogenic actions, such as the reduction of natural habitats in favour of increasingly intensive agriculture, rapid urbanisation, pesticide use and rising temperatures (Dicks et al. 2021, LeBuhn and Vargas Luna 2021, Vasiliev and Greenwood 2021, Nath et al. 2023). This decline has also led to an increase in the spread of emerging infectious diseases (EIDs) caused by pathogens that affect pollinator lifespan (Fürst et al. 2014, Sachman-Ruiz et al. 2015). Given the risks posed by these diseases, studying the transmission of pathogens is of great interest, particularly in terms of transmission routes and the organisms that may be affected, with serious consequences for communities and ecosystem stability (Goulson et al. 2015, Gisder and Genersch 2017). Microorganisms, including bacteria, fungi, protozoa and viruses, manifest in various ways, such as damage to the digestive organs, causing severe malnutrition, malformations and a weakened immune system. These pathologies consequently affect behaviour and orientation, reduce foraging efficiency, and may even lead to the failure of development or death of the individual (Boncristiani et al. 2020, Cilia et al. 2021, Tehel et al. 2022). Historically, studies on bee pathogens began in the hives of *Apis mellifera*, where social individuals are raised at high density and economic interest is significant (Yañez et al. 2020, Nanetti et al. 2021). It is presumed that *A. mellifera* serves as the primary host for pathogen transmission, although this is not yet proven. Similar studies have also been conducted on other commercially managed bees, such as *Bombus*, *Megachile* and *Osmia*, used to promote pollination in greenhouses. Recent studies, however, have shown that the same pathogens commonly found in *A. mellifera* are not only widespread but also replicative in other groups (Nanetti et al. 2021, Tiritelli et al. 2024, Ferrari et al. 2025), particularly wild bees, where more than half of the pathogens known from *A. mellifera* have been detected, many of them co-infected with two or more pathogens in the same individual (Cilia et al. 2022). Wild and honey bees share the same habitats and floral resources, facilitating the spread of pathogens (Alger et al. 2019, Burnham et al. 2021). However, these pathogens have also been found in other hymenopterans such as wasps that prey on bees (Sébastien et al. 2015, Mazzei et al. 2018, 2019), ants that parasitise bee carcasses (Cooling et al. 2017), and even spiders and beetles (Eyer et al. 2009, Levitt et al. 2013, Huang et al. 2019). Currently confirmed transmission routes include direct contact between individuals, particularly pronounced in social insects, oro-faecal transmission, and ingestion of contaminated pollen (Shen et al. 2005, Singh et al. 2010, Tehel et al. 2022), as evidenced by the detection of replicative pathogens in both pupal stages and newly emerged individuals (Cilia et al. 2023). Furthermore, the adaptability of these pathogens promotes their persistence in the environment and on shared trophic resources like flowers. Disease transmission in the environment, through interactions related to resource collection and not solely through direct contact between individuals, has also been demonstrated. The spread of pathogens is related to the environment in which pollinators live: it has been shown that weather conditions and intensive agricultural practices have a greater influence on the presence of abundant and replicative pathogens than on the mass presence of apiaries.

Similarly, functional and biological traits of wild bees, such as being social, soil nesting and oligolecty, are more susceptible to contamination (Tiritelli et al. 2024). Moreover, the global spread of pathogens is facilitated by human activities, such as the trade and transport of colonies beyond their native areas (Owen 2017, Beaurepaire et al. 2020). Although infections are physically evident in *A. mellifera* and *Bombus* specimens, there are also forms of infection that show no physical signs. For example, the (DWV can be present and replicate in an individual without causing any visible damage to the wings, thus not affecting flight. However, there may be non-immediately visible damage at the metabolic or immune system level, especially in cases of coinfection and at the same time, these active forms of infection can still spread to other individuals, resulting in a return infection in host species (Cilia et al. 2021, Gusachenko et al. 2020). While spillover events of pathogens between different arthropod groups are known, their spread, effects and transmission methods are still not fully understood.

Despite the growing evidence that pollinator pathogens circulate widely among wild bees and other flower-visiting insects (Dalmon et al. 2021, Nanetti et al. 2021, Cilia et al. 2022, Deutsch et al. 2023), an entire guild of natural enemies remains almost unexplored in this context: cleptoparasitic and parasitoid cuckoo wasps (Hymenoptera: Chrysididae). These insects are taxonomically diverse and ecologically specialised, with larvae that exploit the nests of solitary bees and wasps and adults that routinely visit flowers for nectar (Pauli et al. 2019). Their life history therefore places them at the intersection of two major epidemiological pathways: 1) intimate, nest-based interactions with their hosts, including physical contact and consumption of host provisions (Ranalli et al. 2026), and 2) horizontal environmental transmission via contaminated floral resources (Alger et al. 2019, Figueroa et al. 2019, Burnham et al. 2021). Yet, no study has assessed whether cuckoo wasps can acquire, maintain, or potentially transmit bee-associated pathogens. Several non-mutually exclusive hypotheses can be formulated regarding pathogen flow from wild bees to their natural enemies. First, within-nest contact offers an even more direct route: cuckoo wasps oviposit inside brood cells, develop in close proximity to host larvae, and cleptoparasitic larvae consume host provisions, potentially enabling efficient transfer of pathogens (Shen et al. 2005, Singh et al. 2010, Cilia et al. 2023). Second, floral transmission may expose adult cuckoo wasps to the same contaminated resources used by bees, particularly in habitats where high pathogen deposition on flowers is documented (Figueroa et al. 2019, Cohen et al. 2022). Generally, cuckoo wasp species feed preferably on plants belonging to the Euphorbiaceae and Apiaceae families (Rosa 2004, Wiesbauer et al. 2020), which may also be visited by other insects, meaning that transmission could occur on these flowers. Third, environmental persistence of infectious particles in nesting substrates may further connect host and parasite populations over time (Adler et al. 2020, Proesmans et al. 2021). Because cuckoo wasps exploit a broad spectrum of bee and wasp hosts, these mechanisms could also facilitate cross-taxonomic spillover, linking pathogen dynamics across multiple hymenopteran guilds (Nanetti et al. 2021). Despite their ecological relevance and ubiquity in bee communities, cuckoo wasps remain overlooked in pathogen research. Whether they act simply as incidental recipients, as reservoirs capable of sustaining replication, or as epidemiological bridges between pollinators and other hymenopterans remains unknown. Addressing this gap is essential for understanding pathogen flow in wild pollinator networks, particularly in landscapes where solitary bees and their enemies co-occur at high densities (Figueroa et al. 2021, Tiritelli et al. 2024).

This study aimed to investigate the presence, abundance, and prevalence of key pathogens known from *Apis mellifera* and wild bees in cuckoo wasps and sympatric hymenopterans. By comparing two environmentally contrasting sites and examining pathogen overlap between cuckoo wasps and their confirmed hosts, we assess whether parasitic interactions represent an unrecognised transmission route and evaluate the broader epidemiological role of Chrysididae within pollinator communities.

Material and methods

Study area

The two study areas were selected based on their suitability as habitats for cuckoo wasps, drawing on both previous knowledge and the authors' expertise. These environments are characterised by sparse grasslands surrounded by woodland areas and located near watercourses, with rocky and sandy zones suitable for hymenopteran nesting. In addition, both habitats provide abundant floral resources as trophic sources. The sampling was conducted in two Italian sites: the first was Palazzo Rossi in northern Italy, in the province of Bologna (site BO, WGS84 coordinates: 44°25′03.8″N, 11°16′35.0″E), and the second was Diga di Arcichiaro, in central-southern Italy, in the province of Campobasso (site CB, WGS84 coordinates: 41°24′55.6″N, 14°31′56.4″E), at elevations of 79 and 860 m a.s.l., respectively. The selection of geographically distant sites with differing altitudes was intentional to ensure sampling diversity while maintaining comparable environmental contexts. Both sites are near freshwater sources: site BO borders the Reno River, and site CB is near an artificial dam. The areas of interest in both locations consist of polyphytic meadows surrounded by shrublands and woodlands (Fig. 1).

Sampling

The sampling focused on capturing cuckoo wasps and their hosts, as well as honey bees and all other hymenopterans present, to obtain a comprehensive sample of the community

Figure 1. Sampling sites in the province of Bologna (BO) and the province of Campobasso (CB), with a focus on land use (Corine Land Cover 2018). Around the site BO, within a 1.5 km radius, there are Artificial surfaces (CLC 112; 121), Forest and semi-natural areas (CLC 311), and Agricultural areas are predominant, specifically 211: Non-irrigated arable land and 242: Complex cultivation patterns. Around the site CB, within a 1.5 km radius, 311: Broad-leaved forest is dominant, along with other Forest and semi-natural areas (CLC 324; 333) and Agricultural areas (CLC 231; 243).

in each habitat. Sampling efforts concentrated on flowers, ground-nesting sites (often in sandy or rocky substrates), and pre-existing cavities in wood. In addition, to attract cuckoo wasps, a sugary mixture was sprayed on low branches of trees and shrubs. Specimens were captured using nets and stored in sterile, empty 2 ml tubes. Sampling was carried out during a single morning session (approximately 4 h) at each site, conducted both in June 2024 on sunny days with maximum temperatures close to 30°C, coinciding with the peak flight period for the sampled taxa. The collected specimens were stored at −80°C until molecular analyses were performed. During the species-level identification phase, before molecular analyses, freezing temperatures were maintained to preserve the integrity of the samples.

Molecular analyses

Each insect was examined individually. All samples were washed in 95% ethanol before extraction to eliminate any external microbiological contamination. The DNA and RNA extraction were performed as previously reported (Cilia et al. 2022, Tiritelli et al. 2024). A quantitative Real-Time PCR (qPCR) analysis was performed to determine the abundance of the same pathogens previously investigated in the CB site (Ranalli et al. 2026). DNA was used to detect *Nosema ceranae* and trypanosomatids (*Lotmaria passim*, *Crithidia mellificae* and *C. bombi*), while RNA was used for viruses (deformed wing virus – DWV; black queen cell virus – BQCV; chronic bee paralysis virus – CBPV; acute bee paralysis virus – ABPV; Kashmir bee virus – KBV, sacbrood virus – SBV). The primers used for the qPCRs are reported in the Supporting information. The qPCR reaction was performed as previously reported (Cilia et al. 2024, Tiritelli et al. 2024). DNA and RNA previously extracted from positive honey bees were employed as positive controls for each pathogen investigated; sterile water was used as a negative control. The number of copies was calculated using a standard curve created for each of the target genes with serially diluted recombinant plasmids containing the pathogen-specific DNA and RNA fragment from 1×10^1 to 1×10^9 copies, as reported in previous (Chantawannakul et al. 2006, Cilia et al. 2018, Mazzei et al. 2018, Buendía-Abad et al. 2021).

Statistical analyses

Pathogen prevalence and abundance were compared between the two sampling sites using the Kruskal–Wallis test, after assessing the non- normality distribution of the data with the Shapiro–Wilk test. In addition, pathogen prevalence and abundance were compared among categories of taxonomic groups (cuckoo wasps, honey bees, wild bees, other hymenopterans) within each site, and at the genus level, also analysed separately for each site. Following the Shapiro–Wilk normality test, group comparisons were conducted using the Kruskal–Wallis test, followed by Dunn's post hoc test with Benjamini–Hochberg correction for pairwise comparisons. Differences in pathogens' abundance and prevalence between male and female individuals were assessed. Shapiro–Wilk test was applied to test normality data distribution. Since most data deviated from normality, non-parametric Wilcoxon rank-sum tests were used to compare male and female groups across species. Statistical comparisons were performed exclusively on cuckoo wasps, and only for the site BO, as all individuals from the second site were female. Virus abundance data were log-transformed ($\log10[x+1]$) to reduce skewness, and all analyses were performed in R ver. 2024.04.1 (www.r-project.org). Besides, a chord diagram was constructed to visualize the interactions between the sampled cuckoo wasp species and the detected pathogens.

Furthermore, the pathogens shared between the cleptoparasitic species of the community and their respective hosts were assessed, based on information available in the literature (Pauli et al. 2019, Wiesbauer et al. 2020, Castillo et al. 2022). Cleptoparasite and parasitoid species have been classified based on the degree of certainty of their interaction with hosts, distinguishing between true cleptoparasite and parasitoid, for which host interactions are well documented, and nest visitors, whose presence in nests has been only occasionally observed and whose actual use or occupation of the nest remains unclear. Only species with a direct match between the two groups were considered, whereas cases in which the host was identified only at the family level were excluded. Two hosts identified at the genus level were included, as in this study they were determined at that taxonomic resolution, although the genus comprises multiple species known to serve as hosts of the corresponding cleptoparasite.

Results

A total of 343 individuals were analysed, including 166 collected from the site CB and 177 from the site BO. At site BO, 22 *Apis mellifera* individuals, 73 wild bees, 29 other hymenopterans and 53 cuckoo wasps (belonging to 8 genera and 21 species) were captured. At the site CB, captures included 7 *A. mellifera*, 6 other hymenopterans, 122 wild bees and 31 cuckoo wasps, all belonging to the species *Chrysis rufitarsis* Brullè, 1833. Among the pathogens screened in the individuals, only *C. mellificae* was not detected in any specimen. KBV was found in just one cuckoo wasp *Hedychrum nobile* at site BO, while at the site CB, it was detected in only two individuals belonging to the genera *Andrena* and *Colletes*. The pathogens most frequently detected across individuals at both sites were *N. ceranae*, CBPV and BQCV.

Sampling sites comparison

When comparing the two sampling sites, pathogen abundance was higher at the site CB for *N. ceranae* ($p\text{-value} < 0.001$), DWV ($p\text{-value} < 0.001$), *L. passim* ($p\text{-value} = 0.045$), and *C. bombi* ($p\text{-value} = 0.002$), whereas ABPV was more abundant at the site BO ($p\text{-value} < 0.001$). Prevalence partially confirmed these results, with higher values of DWV ($p\text{-value} < 0.001$) and *C. bombi* ($p\text{-value} = 0.001$) in individuals from the site CB, while ABPV ($p\text{-value} < 0.001$) and *N. ceranae* ($p\text{-value} = 0.007$) were more prevalent in individuals from site BO (Fig. 2, Supporting information).

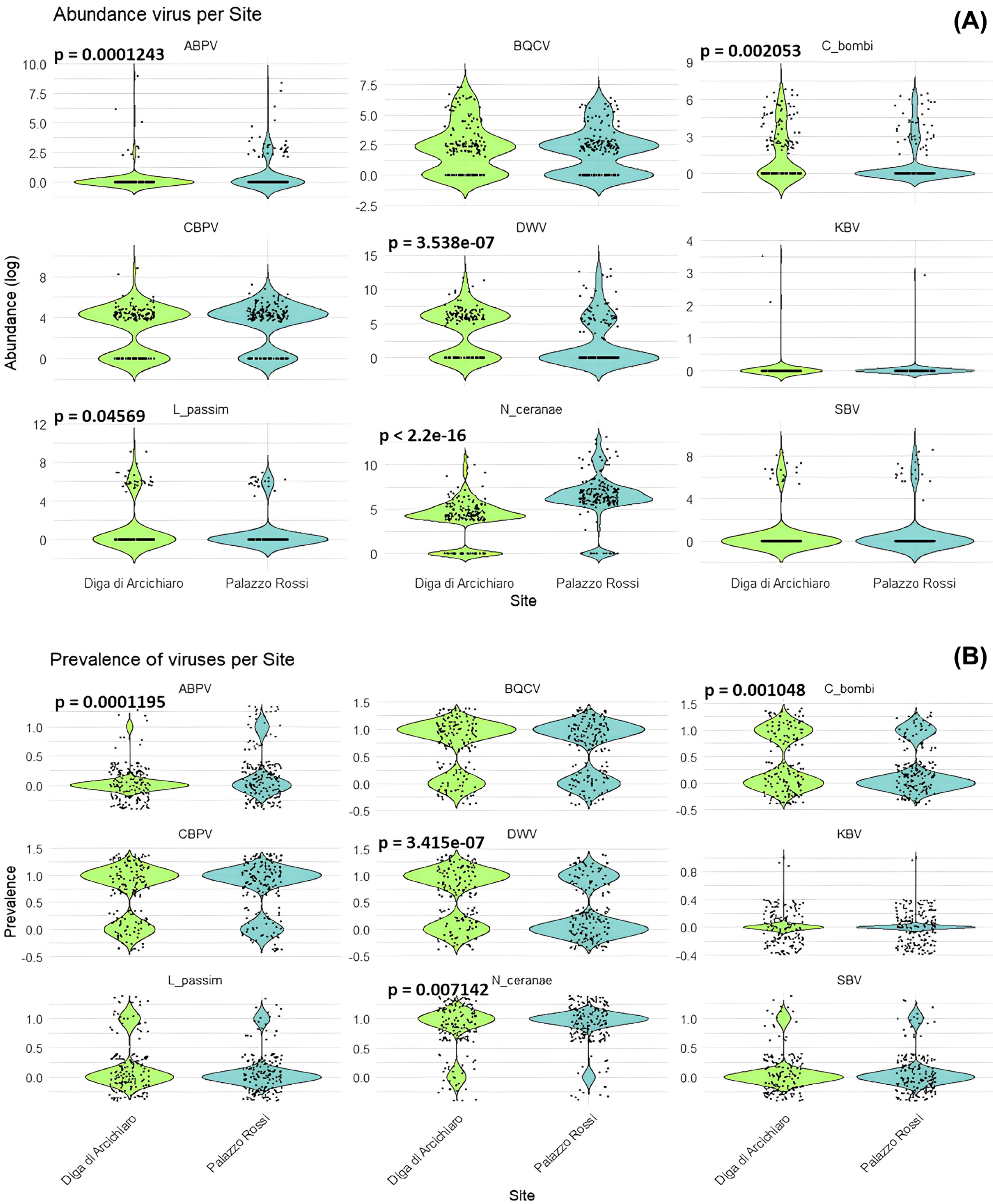


Figure 2. Violin plots were generated to show the abundance (A) and prevalence (B) of each investigated pathogen, compared between the two sampling sites. For comparisons showing significant differences, the corresponding p-value from the Kruskal–Wallis test was reported.

Category level comparison

Analyses by the taxonomic group within each site revealed that cuckoo wasps showed significant differences in abundance for *C. bombi* and DWV at both sites, while BQCV was significant only at the site CB, and *N. ceranae* only at site BO. Prevalence confirmed the significant differences for *C. bombi* and DWV at both sites, whereas CBPV and *L. passim* showed significant differences among groups only at site CB, and BQCV only at site BO.

More specifically, cuckoo wasps consistently showed lower abundance and prevalence of DWV compared to wild bees at both sites (Abundance: site BO p-adj < 0.001, site CB p-adj = 0.002; Prevalence: site BO p-adj < 0.001, site CB p-adj = 0.003). At the site CB, *Chrysis rufitarsis* also had lower values compared to honey bees (Abundance p-adj = 0.002; Prevalence p-adj = 0.005) and other hymenopterans (Abundance p-adj = 0.002; Prevalence p-adj = 0.004). Conversely, for *C. bombi*, both abundance and prevalence were higher in cuckoo wasps than in wild bees at both sites (Abundance: site BO p-adj = 0.007, site CB p-adj = 0.021; Prevalence: site BO p-adj = 0.004, site CB p-adj = 0.015), and prevalence at site BO was also higher than in other hymenopterans (p-adj = 0.029). Additionally, cuckoo wasps had higher BQCV prevalence than wild bees at site BO (p-adj = 0.007). At the site CB, cuckoo wasps showed significantly lower values for BQCV abundance (p-adj = 0.021) and CBPV prevalence (p-adj = 0.038) compared to wild bees. They also showed lower values for *N. ceranae* abundance compared to honey bees (at site BO, p-adj = 0.003), and lower *L. passim* prevalence compared to other hymenopterans (at the site CB, p-adj = 0.048) (Fig. 3, Supporting information).

Genus level comparison

At the genus level, abundance analyses at the site CB revealed that the genus *Chrysis* (*C. rufitarsis*) had lower DWV abundance compared to *Apis mellifera* (p-adj = 0.027) and *Hoplitis laevifrons* (p-adj = 0.041). Conversely, *H. laevifrons* had higher abundance of *L. passim* compared to *Chrysis rufitarsis* (p-adj = 0.005). In this site, cuckoo wasps and *Hoplitis* individuals all belonged to only these two species, respectively *Chrysis rufitarsis* and *Hoplitis laevifrons*, which allows a direct species-level comparison, one being a cleptoparasite of the other (Ranalli et al. 2026). Finally, both abundance and prevalence of KBV confirmed that, at the site CB, individuals of the genus *Hylaeus* had higher values than all other genera, including wild bees, cuckoo wasps, and other hymenopterans. At site BO, genus-level analyses did not yield significant results, except for *N. ceranae* abundance, which was lower in *Lasioglossum* compared to *A. mellifera* (p-adj < 0.001) and *Megachile* (p-adj = 0.031) (Supporting information).

Cuckoo wasp species infection and sex comparison

No significant differences were observed between males and females in either pathogens' abundance or prevalence, except for CBPV abundance, which was higher in males than in females (p-value = 0.038). KBV was absent in the cuckoo wasps included in this analysis and was therefore excluded (Supporting information).

A schematic representation was created solely for visualisation purposes, in order to better understand the interactions between the cuckoo wasp species and the pathogens detected in the specimens. In this diagram, the two sites were merged, bearing in mind that the species *Chrysis rufitarsis* was the only one collected at the site CB (Fig. 4).

The number of pathogens shared between each cleptoparasitic species and its respective host are summarized in Table 1. It also reports the number of known hosts for each species and the number of pathogens detected at the species level, rather than at the level of individual samples. For cleptoparasitic species sampled in this study whose hosts were not collected, the corresponding host species are nevertheless listed in the Supporting information. The interaction between *C. rufitarsis* and *H. laevifrons* was observed exclusively at the site CB, where the two species not only carried eight out of nine pathogens, but shared all of them. Similarly, at the site BO, the cleptoparasitic species shared the full set of pathogens with their respective hosts, except for *Hedychrum* species parasitising *Cerceris*, which shared only a subset of pathogens.

Discussion

This study provides the first evidence that cuckoo wasps (Hymenoptera: Chrysididae), a family of cleptoparasitic and parasitoid insects, can host a diverse range of pathogens traditionally associated with honey bees and wild pollinators. Until now, cuckoo wasps have been entirely absent from the debate on pollinator health and pathogen transmission. The results of this investigation, however, demonstrate the presence of *N. ceranae*, trypanosomatids, and several viruses in cuckoo wasp species across different sites. These findings substantially extend the known host range of the pollinator pathogens (Alger et al. 2019, Nanetti et al. 2021, Piché-Mongeon and Guzman-Novoa 2024), suggesting that cuckoo wasps may participate in the epidemiological networks that link bees, wasps and other hymenopterans.

Beyond the novel findings on cuckoo wasps, the data also provided insight into pathogen circulation within the broader pollinator community, particularly the relationships among honey bees, wild bees, and other hymenopterans. Consistent with previous work showing that *A. mellifera* often acts as a major epidemiological hub in shared floral networks (Fürst et al. 2014, Alger et al. 2019, Cilia et al. 2022), the investigated honey bees in this study carried a high prevalence of *N. ceranae*, ABPV and DWV, and in several cases reached higher pathogen abundance than sympatric wild bees. These findings corroborate the hypothesis that managed honey bee colonies can increase pathogen pressure on local communities, especially in lowland or anthropogenic landscapes (Piot et al. 2022, Maurer et al. 2024). However, wild bees also showed substantial levels of infection and in some cases harboured pathogens at equal or higher abundance than honey bees, reinforcing that spillover is not unidirectional

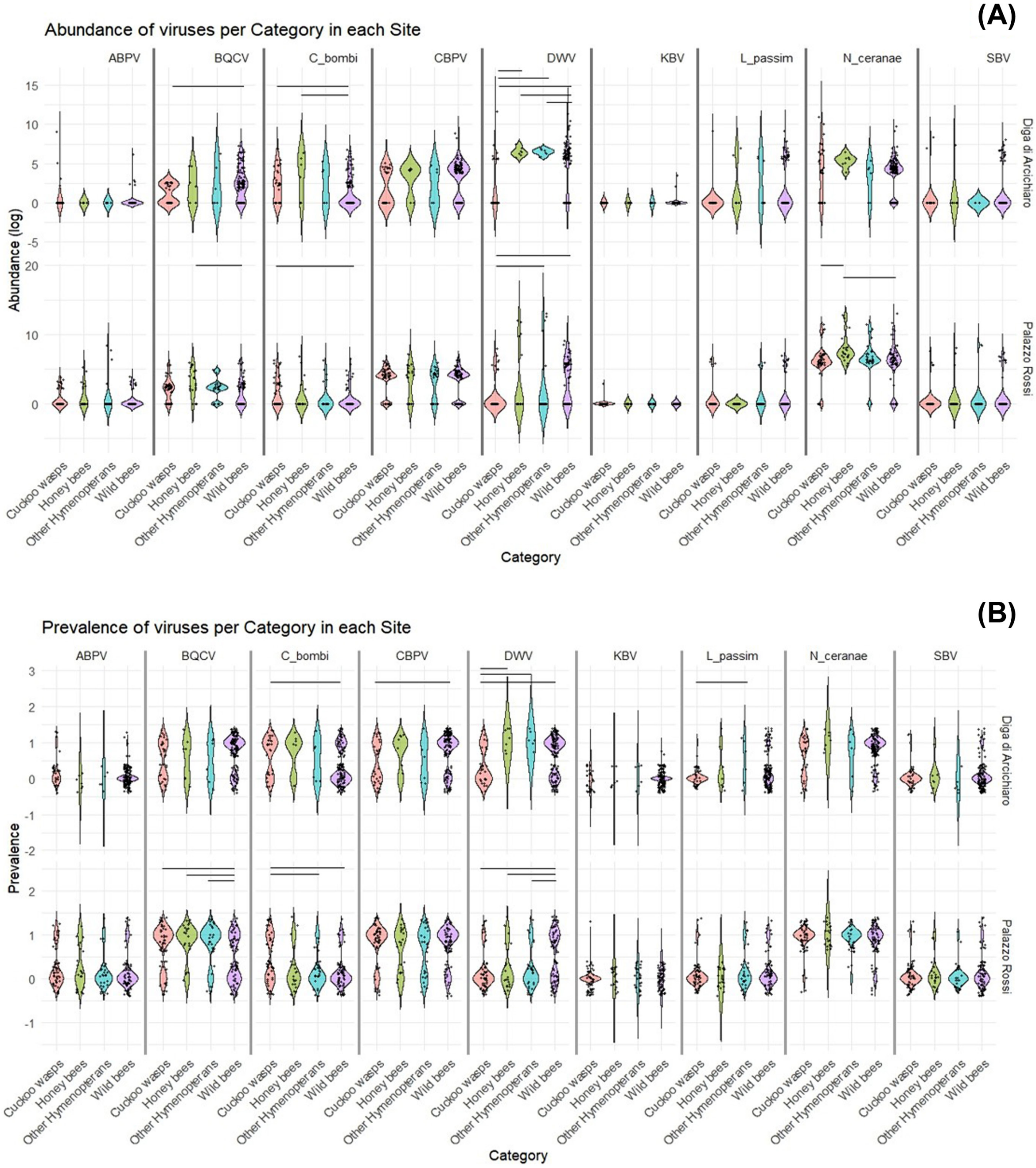


Figure 3. Violin plots were generated to show the abundance (A) and prevalence (B) of each investigated pathogen, compared at the taxonomic group level across the two sampling sites. For comparisons showing significant differences, a bar was included between the groups.

and that wild bees can act as relevant reservoirs for certain pathogens (Deutsch et al. 2023, Sagastume et al. 2025). The pronounced differences in pathogen profiles between the two sites, higher DWV and *C. bombi* at the montane site, versus higher *N. ceranae* and ABPV at the lowland one, suggest that ecological context and landscape structure modulate pathogen circulation more strongly than the presence of honey bees alone (Proesmans et al. 2021, Tiritelli et al. 2024).

The patterns observed in non-cuckoo wasps provide further evidence of cross-guild pathogen flow. Predatory and nectar-feeding wasps carried several of the pathogens detected in bees, including viruses and trypanosomatids, in line with studies reporting widespread cross-taxa transmission among Hymenoptera (Mazzei et al. 2018, 2019, Nanetti et al. 2021). These wasps may acquire pathogens through multiple pathways: consumption of infected prey, contact with contaminated nesting material, or exploitation of shared floral resources. Their infection profiles can therefore reflect both their trophic role and their degree of floral overlap with bee communities. In this study, certain

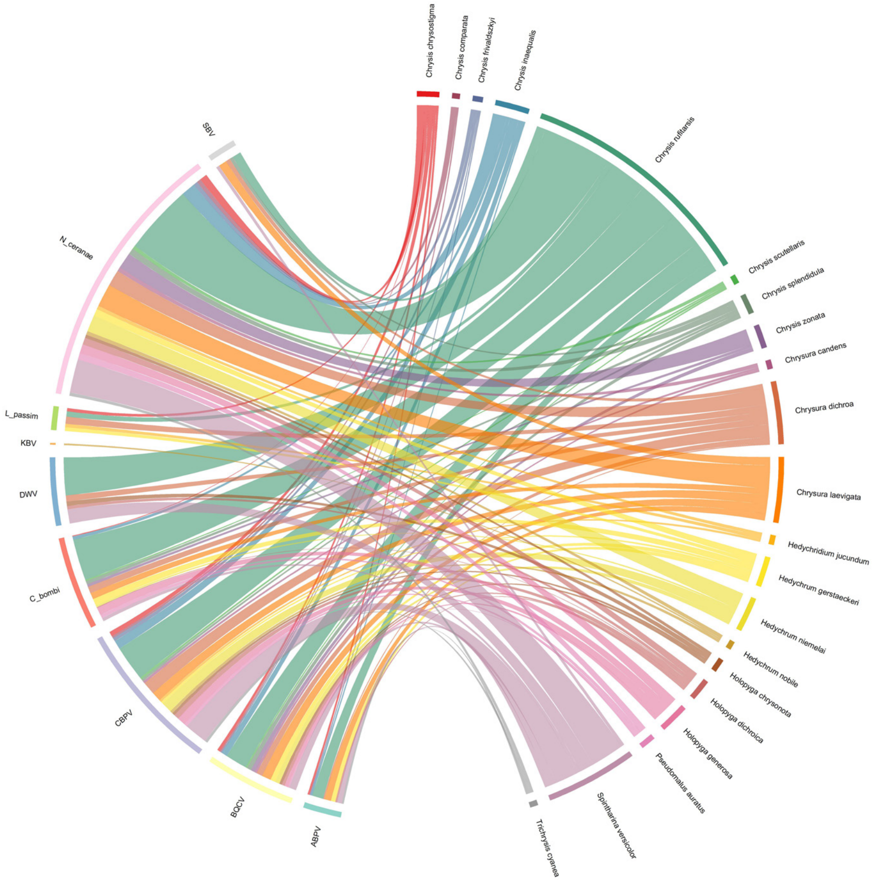
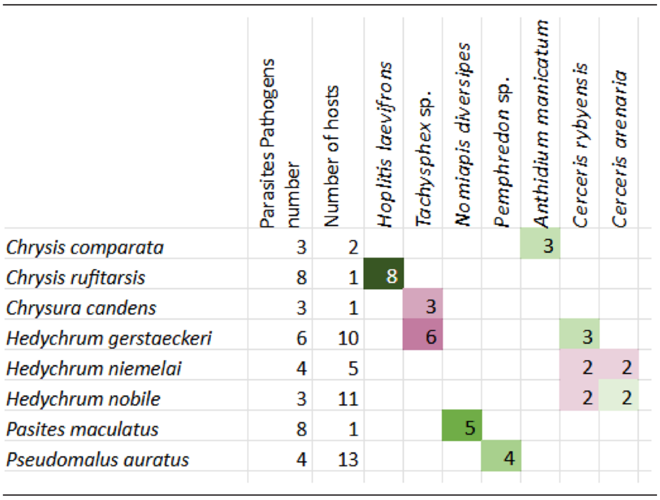


Figure 4. Diagram of the interactions between cuckoo wasp species and identified pathogens.

pathogens such as *L. passim* and CBPV showed comparable prevalence between wasps and wild bees, supporting the idea that non-bee hymenopterans can participate actively in pathogen persistence rather than functioning as accidental recipients. Given their frequent predation or scavenging on bees, some of these species may also act as secondary vectors or reservoirs, as previously suggested for genera such as *Vespa* or *Vespula* (Sébastien et al. 2015, Cooling et al. 2017, Quinn et al. 2018, Gabín-García et al. 2021, Cilia et al. 2024, Power et al. 2024).

Table 1. Number of pathogens shared between cleptoparasitic species and their respective hosts. Reliable interactions are shown in green, while the interactions between nesting-visitors and hosts are reported in pink.



	Parasites Pathogens number	Number of hosts	*Hoplitis laevifrons*	*Tachysphex sp.*	*Nomiapis diversipes*	*Pemphredon sp.*	*Anthidium manicatum*	*Cerceris rybyensis*	*Cerceris arenaria*
Chrysis comparata	3	2					3		
Chrysis rufitarsis	8	1	8						
Chrysura candens	3	1		3					
Hedychrum gerstaeckeri	6	10		6				3	
Hedychrum niemelai	4	5						2	2
Hedychrum nobile	3	11						2	2
Pasites maculatus	8	1			5				
Pseudomalus auratus	4	13				4			

Taken together, these results depict a pollinator–parasite network in which honey bees, wild bees, cuckoo wasps, and other hymenopterans are epidemiologically interconnected. No single taxon operates in isolation: rather, pathogens circulate across multiple functional groups through overlapping foraging niches, predatory or parasitic interactions, and environmental persistence. The inclusion of cuckoo wasps in this framework is therefore not only novel but also necessary, as they represent an additional, and previously overlooked, bridge linking floral and nest-associated transmission routes. A central outcome of this study is the high overlap of pathogens between cuckoo wasps and their hosts. In the case of *Chrysis rufitarsis* and its host *Hoplitis laevifrons*, nearly the full set of screened pathogens was shared (Ranalli et al. 2026). This striking congruence indicates that the intimate host–parasite association inherent to cuckoo wasps' biology facilitates direct pathogen transfer (Figueroa et al. 2021, Tiritelli et al. 2024). Unlike transmission through shared floral resources or contaminated pollen (Figueroa et al. 2019, Pinilla-Gallego et al.

2022, Maurer et al. 2024), the cuckoo wasp–host interaction involves close contact during oviposition and larval development, potentially enabling pathogens to bypass environmental dilution and move directly between species. Reliable host associations for *H. niemelai* include *Cerceris quadrifasciata* and *C. quinquefasciata*, whereas *H. nobile* is consistently associated with *C. arenaria*, and *H. gerstaeckeri* with *C. rybyensis*, *C. ruficornis* and *C. sabulosa* (Pauli et al. 2019, Wiesbauer et al. 2020). Additional host records have been reported in the literature, including *C. arenaria, C. ruficornis* and *C. rybyensis* for *H. niemelai*, and *C. quadrifasciata* and *C. rybyensis* for *H. nobile* (Rosa 2006). However, these latter associations have been regarded as potentially unreliable and are likely to reflect cases of cuckoo wasp misidentification or observational bias rather than true host–parasitoid relationships. Despite this taxonomic uncertainty, the three *Hedychrum* species are known to be syntopic, frequently cooccurring at the same sites and actively inspecting nests of multiple *Cerceris* species. Consequently, some erroneous host associations reported in the literature may stem from field observations of cuckoo wasp individuals visiting or entering nests of non-host *Cerceris* species. Importantly, even in the absence of confirmed parasitism, such nest inspection behaviour may still be epidemiologically relevant. Physical contact with nest structures, provisions, or brood during these inspections could facilitate exposure to, and potential transmission of, pathogens among taxa, irrespective of strict host specificity. A comparable situation applies to historical records of *Tachysphex* species reported as hosts of *H. gerstaeckeri* and *Chrysura candens* (Trautmann 1927, Lefeber and Petit 1970, Leclercq 1988), which were subsequently considered unreliable by Pauli et al. (2019). As with *Cerceris–Hedychrum* associations, these records may reflect observations of cuckoo wasps entering *Tachysphex* nests for inspection rather than evidence of true parasitism. Nevertheless, such interactions may still represent meaningful opportunities for pathogen exchange, supporting the view that pathogen transmission pathways in hymenopteran communities extend beyond strict host–parasitoid relationships and encompass a broader spectrum of ecological contacts.

Nevertheless, cuckoo wasps do not simply mirror their hosts' infection patterns. While DWV prevalence and abundance were consistently lower than in wild bees and *A. mellifera*, in which the virus is completely spread (Martin and Brettell 2019, Brettell et al. 2020, Gusachenko et al. 2020, Paxton et al. 2022, Streicher et al. 2024), other pathogens, such as *C. bombi* and BQCV, reached higher prevalence in cuckoo wasps than in sympatric wild bees. This suggests that cuckoo wasps may act as selective reservoirs or even amplifiers for particular pathogens. Given that cuckoo wasps exploit a wide taxonomic spectrum of hosts, including solitary bees, wasps and sawflies, their epidemiological relevance could extend across multiple guilds of hymenopterans.

The ecological and environmental context also plays a critical role in shaping these dynamics. Pathogen prevalence and abundance are known to respond to landscape composition, climatic variability, and agricultural intensification, often more strongly than to the density of managed colonies (Proesmans et al. 2021, Piot et al. 2022, Tiritelli et al. 2024, Wham et al. 2024, McAfee et al. 2025). In this study, site-level differences in pathogen profiles were consistent with this pattern: the lowland site (site BO, Palazzo Rossi) exhibited higher levels of *N. ceranae* and ABPV, while the montane site (site CB, Diga di Arcichiaro) showed elevated prevalence of DWV and *C. bombi*. Such contrasts highlight the interplay between environmental conditions, such as temperature, humidity and floral availability, and the epidemiology of pathogens in pollinator communities. Environmental persistence of infectious particles on flowers (Adler et al. 2020, Burnham et al. 2021, Cohen et al. 2022) and in nesting substrates further reinforces the potential for cross-species transmission, especially in diverse habitats where cuckoo wasps and their hosts overlap spatially and temporally.

Cuckoo wasps are particularly interesting because they connect two epidemiological areas. As adults, they forage on flowers, entering the same horizontal transmission network as bees and other pollinators (Wiesbauer et al. 2020). As larvae, they develop as parasitoids or cleptoparasites within the nests of solitary bees or wasps, establishing vertical or direct contact-based transmission routes (Wurdack et al. 2015). This dual life history makes cuckoo wasps potential 'epidemiological bridges,' linking host species that may otherwise have limited direct interaction. In ecosystems where multiple pollinator and parasitoid species coexist, cuckoo wasps may therefore contribute to maintaining pathogen circulation and enabling spillover events across taxonomic boundaries.

From a community ecology perspective, these findings strengthen the view that pollinator pathogens must be regarded as community-level pathogens (Goulson et al. 2015, Gisder and Genersch 2017, Dalmon et al. 2021, Cilia et al. 2022, Deutsch et al. 2023, Sagastume et al. 2025). They do not circulate exclusively within *A. mellifera* populations but are embedded within broader insect networks, involving wild bees, predatory wasps, ants, and, as this study shows for the first time, parasitic cuckoo wasps. Importantly, the detection of active, replicative forms of pathogens in cuckoo wasps suggests that they are not merely contaminated individuals but may support pathogen persistence and transmission.

The recognition of cuckoo wasps as part of this network carries several implications. First, it highlights the need to include parasitic taxa in pathogen monitoring and biodiversity surveys, especially in natural and semi-natural habitats where they are common. Second, it raises the possibility that cuckoo wasps, given their specific host spectrum and ecological sensitivity, could serve as bioindicators of pathogen pressure in disturbed ecosystems (Drezen et al. 2022, Lorenzi et al. 2022). Third, it prompts new questions about the evolutionary consequences of pathogen circulation through parasitic lineages: could cuckoo wasps act as refuges for pathogens when host densities are low, or as amplifiers when host communities are diverse and abundant?

Conclusions

In conclusion, this study identifies cuckoo wasps as novel players in pollinator pathogen ecology. By combining parasitic and nectar-feeding behaviours, they occupy a unique position in the epidemiological web, bridging different hosts and environments. These first findings call for further research across multiple cuckoo wasp genera, habitats, and climatic regions. Future work should integrate molecular screening, experimental infection assays, and ecological modelling to clarify whether cuckoo wasps are incidental spillover hosts, stable reservoirs, or even vectors influencing the spread of pathogens in pollinator communities. Understanding their role will be essential not only for pollinator health but also for preserving the stability and resilience of ecosystems under increasing anthropogenic pressure.

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Author contributions

Rosa Ranalli: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Paolo Rosa**: Data curation (equal); Formal analysis (equal); Investigation (equal); Writing – review and editing (equal). **Simone Flaminio**: Data curation (equal); Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Marco Selis**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Loris Colacurcio**: Formal analysis (equal); Investigation (equal); Writing – review and editing (equal). **Giovannni Cilia**: Conceptualization (equal); Data curation (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.mkkwh71f7 (Ranalli et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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